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Global loss of avian evolutionary uniqueness in urban areas

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Abstract

Urbanization, one of the most important anthropogenic impacts on Earth, is rapidly expanding worldwide. This expansion of urban land-covered areas is known to significantly reduce different components of biodiversity. However, the global evidence for this effect is mainly focused on a single diversity measure (species richness) with a few local or regional studies also supporting reductions in functional diversity. We have used birds, an important ecological group that has been used as surrogate for other animals, to investigate the hypothesis that urbanization reduces the global taxonomical and/or evolutionary diversity. We have also explored whether there is evidence supporting that urban bird communities are evolutionarily homogenized worldwide in comparison with nonurban ones by means of using evolutionary distinctiveness (how unique are the species) of bird communities. To our knowledge, this is the first attempt to quantify the effect of urbanization in more than one single diversity measure as well as the first time to look for associations between urbanization and phylogenetic diversity at a large spatial scale. Our findings show a strong and globally consistent reduction in taxonomic diversity in urban areas, which is also synchronized with the evolutionary homogenization of urban bird communities. Despite our general patterns, we found some regional differences in the intensity of the effect of cities on bird species richness or evolutionary distinctiveness, suggesting that conservation efforts should be adapted locally. Our findings might be useful for conservationists and policymakers to minimize the impact of urban development on Earth's biodiversity and help design more realistic conservation strategies.

Keywords: biodiversity, biotic homogenization, birds, evolutionary distinctiveness, human-induced environmental change, urban ecology

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Introduction

The expansion of urban areas is considered one of the most important anthropogenic impacts on the Earth's ecosystem (Foley *et al*., 2005; Groom *et al*., 2006), dramatically changing natural habitat structure, ecosystem functioning, and life's biodiversity (Grimm *et al*., 2008a; Gaston, 2010; Forman, 2014; Gil & Brumm, 2014). Urban areas are growing proportionally faster than any other form of land cover (United Nations, 2012) as urban-dwelling human population is increasing by 1 million per week (Seress & Liker, 2015). By 2030, there is an expected 200% increase in global urban land cover in comparison with the year 2000 (Fragkias *et al*., 2013). It is not surprising therefore that the process of urbanization and its environmental impact is now recognized as a major global challenge (United Nations, 2016) and has attracted increased attention in the past decades (McDonnell *et al*., 2016).

Organisms can exhibit different responses to urbanization (McDonnell & Hahs, 2008), and while a few species are beneficiated by cities (i.e., urban exploiters), many more are negatively affected by this landscape change (i.e., urban avoiders; Blair, 1996; Sol *et al*., 2014). In fact, one of the most important ecological effect of urbanization is the overall decrease in taxonomic diversity (Marzluff, 2001; Chace & Walsh, 2006; McKinney, 2008; Newbold *et al*., 2015). This loss of biodiversity is caused by both changes in the abiotic (i.e., habitat loss Clergeau *et al*., 1998; Kühn & Klotz, 2006) and biotic component of the environment (i.e., invasive species Grimm *et al*., 2008b; Luck & Smallbone, 2010; Garcillán *et al*., 2014) which lead to the extirpation of native organisms and can drive the homogenization of biotas in cities (McKinney, 2006; Devictor *et al*., 2007; Morelli

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et al., 2016). This issue is even more relevant considering that this negative impact of urban land-cover expansion on biodiversity is expected to increase globally in the future due to the selective expansion of towns and cities in key biodiversity hot spots (Seto *et al*., 2012). This scenario has led to consider urbanization as a major topic in conservation biology (Miller & Hobbs, 2002; McKinney, 2006) and has also attracted the attention of politics and policymakers (Secretariat of the Convention on Biological Diversity, 2012; Elands *et al*., 2015). The recently published World Cities Report (United Nations, 2016) states that one of the main challenges regarding urbanization is related to 'minimizing the negative impacts of land transformations in the use of resources, biodiversity, and ecosystems'.

However, previous knowledge on the effect of the urban land-cover expansion on biodiversity is mainly based on a single measure of biodiversity, species richness (Marzluff, 2001; Chace & Walsh, 2006; McKinney, 2008), while very little attention has been paid to other diversity measures (Devictor *et al*., 2008; Knapp *et al*., 2008; Morelli *et al*., 2016). Biodiversity refers to variation at all levels of biological organization and includes three main elements (genetic, ecological, and organismal diversity), and although species richness is the most commonly used measure of biodiversity, it has important restrictions to capture certain components of biodiversity (Gaston & Spicer, 2004). Another important issue directly related to the biodiversity loss driven by urbanization is the process of biotic homogenization (Clergeau *et al*., 2006; McKinney, 2006). Irrespective of the biome, urbanization creates habitats with particular physical characteristics across locations (Groffman *et al*., 2014) that favor some synurbic species (those particularly associated to urban areas) while reducing local species (Francis & Chadwick, 2012). And, at the same time, it favors transportation of non-native species around the world (McKinney, 2008). This process tends to create similar genetic, taxonomic, and/or functional biotas all over the world (Olden *et al*., 2004; Devictor *et al*., 2008; Knop, 2016) and acts mainly through the extinction of native species and introduction of alien organisms (Olden & Poff, 2003; Klotz & Kühn, 2010; Shochat *et al*., 2010; Čeplová *et al*., 2015).

The evolutionary distinctiveness or uniqueness is a measure of evolutionary history, more related to the genetic element of biodiversity. Basically, it measures how isolated a species is in a phylogenetic tree and represents uniquely divergent organisms (Isaac *et al*., 2007; Jetz *et al*., 2014). Consequently, this measure of phylogenetic diversity can play an important role to establish conservation priorities (Isaac *et al*., 2007; EDGE of Existence, 2015). For instance, recent recommendations in nature conservation optimization encourage the use of measures of phylogenetic diversity alongside species richness (Winter *et al*., 2012; Monnet *et al*., 2014). In relation to urbanization, two recent regional-scale studies have found that urban areas hold communities with low levels of phylogenetic diversity. Čeplová *et al*. (2015) showed that the phylogenetic diversity of plant communities in Central Europe was lower than random. Similarly, Morelli *et al*. (2016) has found a significant reduction in evolutionary distinctiveness of urban bird assemblages in comparison with rural ones (Morelli *et al*., 2016). This study did not detect significant differences in bird species richness between the two habitats, which strongly supports the need for exploring other measures of biodiversity, to gain a more complete picture of the ecological effects of urbanization. However, even if these two studies suggest the phylogenetic homogenization of European bird and plant assemblages due to urbanization (Čeplová *et al*., 2015; Morelli *et al*., 2016), there has not been a general attempt to explore these patterns at a larger-scale yet. The global-scale perspective is particularly relevant because even though urbanization is a worldwide process (Grimm *et al*., 2008a), the majority of papers that explore how urbanization affects biodiversity are geographically restricted preventing generalization of many observed patterns (Pautasso *et al*., 2011; Müller *et al*., 2013; Seress & Liker, 2015). Moreover, urban land-cover change can also have different impacts depending on the particular characteristics of the region (McKinney, 2002; Grimm *et al*., 2008b). In fact, some particular areas are expected to be affected more deeply than others by urbanization (Seto *et al*., 2012) and, therefore, the comparison among regions will help us to establish conservation priorities more accurately.

Here, using birds and a large spatial scale approach, we (i) investigate whether urban areas from different continents are associated with lower biodiversity measures (species richness and evolutionary distinctiveness) than nonurban areas and (ii) look for evidence supporting that urban landscapes are associated with phylogenetically homogenized communities worldwide. We have used birds as our model group because they are key components of ecosystems (Şekercioğlu, 2006), good bioindicator for other taxa (Rodrigues *et al*., 2007), with a widely validated phylogeny (Jetz *et al*., 2012; Prum *et al*., 2015) and well studied within the urban ecology context (Marzluff *et al*., 2001; Lepczyk & Warren, 2012; Gil & Brumm, 2014), thus offering the opportunity to compile a geographically wide database while testing our hypotheses in relation to an ecological relevant group.

Materials and methods

Bibliographic research and selection of studies

We did an exhaustive literature search in Web of Science, Google Scholar, and SmartCat (www.rug.nl/bibliotheek/smartcat/) using different combinations of the following terms: 'bird*', 'assemblages' and 'urban*'. We look for studies presenting information on the avian community of both urban and nonurban habitats from the same area. If possible, we collected data from the wildland habitat sensu Marzluff *et al.* (2001) as the nonurban habitat, although it was not always available and in some cases it represented an agricultural (rural) land cover, according to definitions provided by Marzluff *et al.* (2001). Given that agricultural habitats usually present lower avian biodiversity values than native ones (e.g., Sinclair *et al.*, 2002; Billeter *et al.*, 2008), we consider our procedure to be conservative. We discarded studies not showing the complete bird community (i.e., only most common species) or those presenting information from only one of the two habitats (i.e., only urban species). This study selection criterion allowed us to collect data on urban and nonurban bird communities that were obtained following the same field method, during the same time period and by the same field observer, thus standardizing for many potential confounding factors in this kind of comparative study. Some papers presented information from several locations within an urban gradient. In such cases, we extracted the data of those two locations that better represented the urban and wildland/rural habitats sensu Marzluff *et al.* (2001).

From each study, we extracted the following information: (i) urban bird assemblage, (ii) nonurban bird assemblage, (iii) continent, (iv) country, (v) site, (vi) latitude, (vii) longitude, and (viii) whether the data correspond to the breeding, nonbreeding season, or both. Coordinates were obtained directly from the paper or from Google Maps if not available in the study.

Biodiversity and evolutionary distinctiveness

From each study, we calculated two diversity values (species richness and evolutionary distinctiveness) for each habitat. The bird species richness was calculated as the highest number of species observed in each location as it is a basic surrogate for taxonomic diversity (Magurran, 2004). The evolutionary distinctiveness (ED) score is a measure of richness in phylogenetic diversity (Tucker *et al.*, 2016) based on the uniqueness of a species (Redding *et al.*, 2010; Jetz *et al.*, 2014). The ED score is calculated considering the sum of all phylogenetic branch lengths connecting species (Cadotte *et al.*, 2008, 2012) and by applying a value to each branch equal to its length divided by the number of species subtending the branch (Isaac *et al.*, 2007). Using the ED score for each bird species present in a community, we estimated the community evolutionary distinctiveness (CED) as the average ED considering all species belonging to the community. The CED is a measure of divergence, related to the phylogenetic isolation (Tucker *et al.*, 2016). This procedure has also the advantage to make this variable independent from the number of species present in each community, optimizing the comparison among many studies. Furthermore, the highest ED score of a bird species present in the assemblage was labeled as the maximum ED for this bird community (max ED).

Statistical analyses

We used generalized linear mixed models (GLMMs) to study the patterns of bird richness, CED and max ED in relation to urban and nonurban habitats, latitude and longitude modeled as fixed effects. We decided to include these geographical predictors as they can be related to large-scale changes in biodiversity (Mannion *et al.*, 2014; Morelli *et al.*, 2016). Country (groups = 17) and season (group = 3) were included as random effects to account for possible consistent differences among countries or in relation to breeding or nonbreeding period. The use of random effects permits statistical tests when some observations can be correlated. In the particular study case, it is useful in order to remove any potential differences related to methods or sampling effort among studies in each country.

Models using CED and max ED as response variable were fitted by maximum likelihood, using the package 'lme4' in R (Bates *et al.*, 2014), while models using bird species richness as response variable were fitted assuming a Poisson distribution after having explored the variable distribution as suggested in Box & Cox (1964) using the package 'MASS' (Venables & Ripley, 2002) and 'glmmADMB' in R (Fournier *et al.*, 2012; Skaug *et al.*, 2013). In this study, the Akaike information criterion (AIC) was calculated to determine the models that 'best' explained variation in the data (Burnham & Anderson, 2002). The model selection and multimodel inference were performed using the package 'AICcmodavg' in R (Mazerolle, 2016). The best model was selected considering both lowest AIC and large Akaike weights, because this model had the strongest support for data (Mazerolle, 2016). The confidence intervals for the significant variables selected in the best model were calculated by the Wald method from the package 'MASS' (Venables & Ripley, 2002). All statistical tests were performed with R software (R Core Team, 2016).

Results

Our literature search provided us with 26 studies that matched our strict search criteria. We identified a total of 665 bird species from 28 paired urban vs. nonurban locations from 17 countries and four continents (Fig. 1, Table S1). The list of all bird species used in this study in both urban and nonurban sites, with their ED score, is provided in the Table S2.

All three diversity measures (bird richness, CED, and max ED) showed significantly lower values in urban than in nonurban habitats for the global analyses (Table 1; Fig. 2). The confidence intervals for the predictor 'habitat' always ranged across negative values for all three response variables (Table 1). Based on our

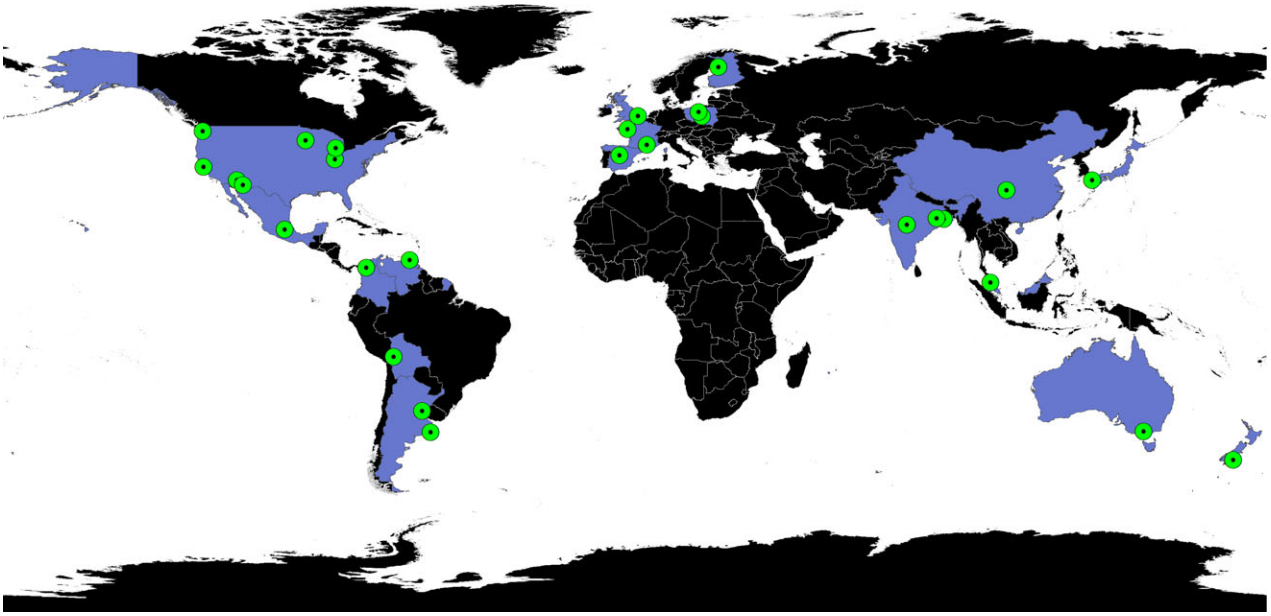

Fig. 1 Location of the 28 cities (and their corresponding nonurban areas) used in our study (green dots) distributed in 17 countries (blue) from four different continents. For coordinates and city names involved in each study, see Table S1. [Colour figure can be viewed at wileyonlinelibrary.com]

Table 1 Results of fixed-effect parameters in the generalized linear mixed models (GLMMs), accounting for variation in bird richness, community evolutionary distinctiveness (CED), and max ED in relation to urban or nonurban habitat

Source of variation	Estimate	CI	SE	*t*/*z*	*P*
Bird richness					
Habitat: urban	−0.55	−0.65, −0.45	0.05	−10.6	2E-16
CED					
Habitat: urban	−0.56	−1.05, −0.08	0.23	−2.3	0.002
max ED					
Habitat: urban	−4.75	−9.29, −0.26	2.3	−2.1	0.038

CI, confidence interval (lower/higher); SE, standard error. Only significant variables are shown in the table.

statistical procedures, these differences were independent of the country or season as we included them as random factors. This general pattern is also maintained after grouping the results of all studies by continent for both bird species richness (Fig. 3) and CED (Fig. 4). Then, the urban biodiversity was lower than the nonurban biodiversity in all continents. However, we found some interesting results with South American bird communities showing the largest difference in species richness but the smallest difference for CED (Figs 3 and 4). Oceania also presented remarkable results with a similar difference for bird species richness between habitats as that observed in other continents, but the largest difference in CED (Figs 3 and 4).

Longitude and latitude did not significantly improve the proportion of species richness, CED, or max ED variance explained by the model including only habitat as a predictive variable (Table S3) suggesting that those geographical predictors are of little importance regarding our data. This result supports the generality of our findings and highlights that the main factor explaining variation in avian CED is the urban vs. nonurban comparison. The list of evaluated models, with the number of predictors considered, delta AIC values, and AIC weights for each one is provided in Table S3.

Discussion

Our findings highlighted the fact that urbanization significantly reduced both species richness and evolutionary distinctiveness worldwide (Fig. 2), supporting the assumption that the expansion of urban areas reduces biodiversity. Considering that urbanization is a similar process acting worldwide (McKinney, 2006; Grimm *et al.*, 2008a), the large-scale geographical distribution of our database (including cities in four continents) and the nonsignificant effect of geographical variables (latitude and longitude) in any of our biodiversity

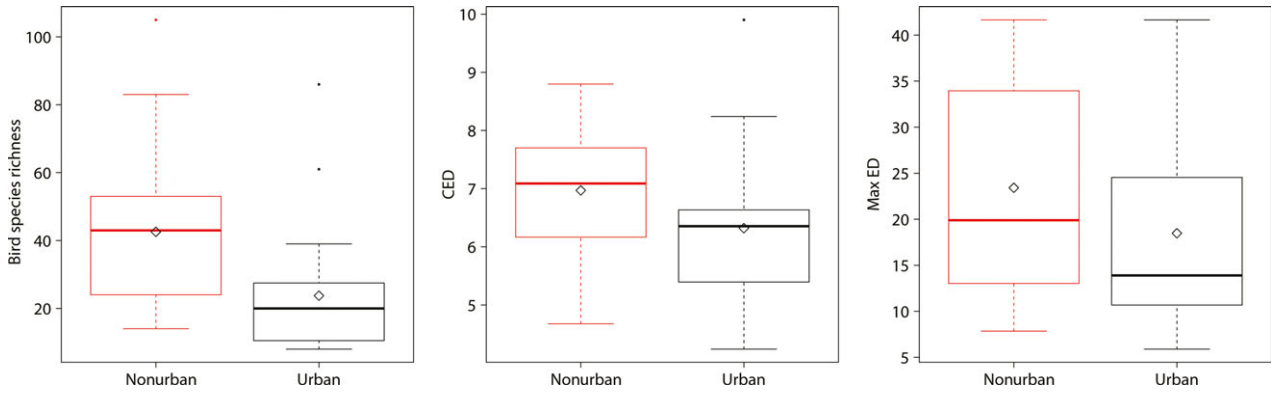

Fig. 2 Comparison of bird species richness, community evolutionary distinctiveness (CED), and maximum evolutionary distinctiveness (max ED) between urban and nonurban habitats. The *y*-axis represents the estimated variable. The box plots show the median (bar in the middle of rectangles), mean (rhombus), upper and lower quartiles, maximum and minimum values (vertical dashed lines), and outliers. [Colour figure can be viewed at wileyonlinelibrary.com]

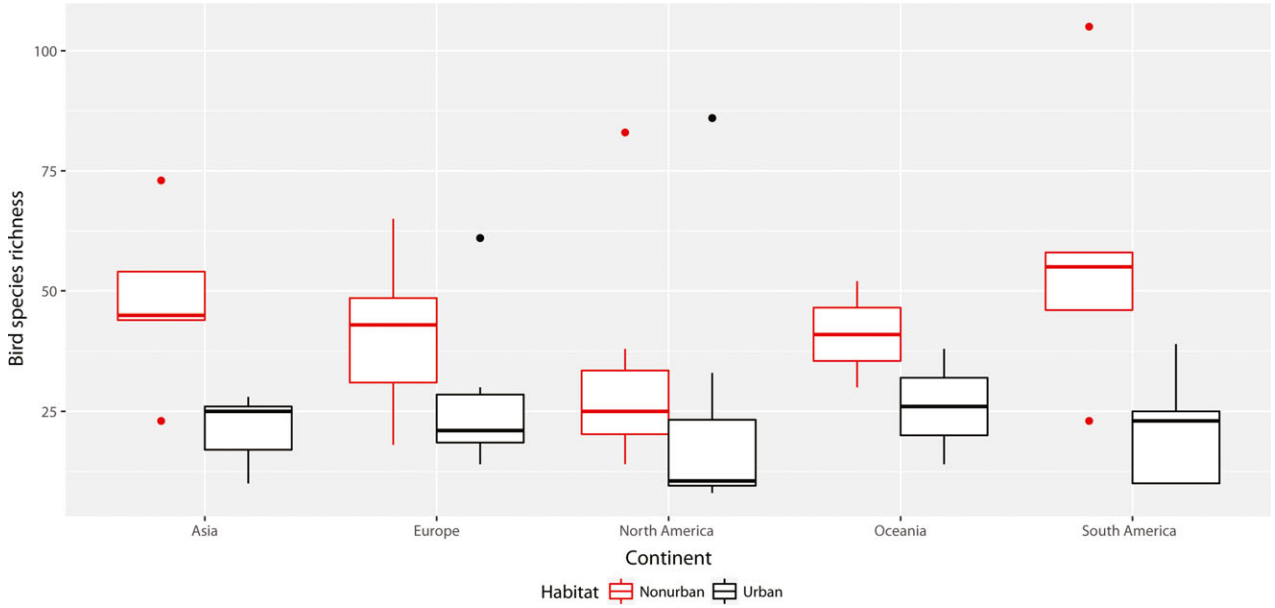

Fig. 3 Comparison of bird species richness between habitats in each continent. The *y*-axis represents the estimated variable. The boxplots show the median (bar in the middle of rectangles), upper and lower quartiles, maximum and minimum values (vertical lines), and outliers. [Colour figure can be viewed at wileyonlinelibrary.com]

measures, we believe that our results could be reasonably considered representative of a global pattern. The result on species richness matches with previous findings on birds (Marzluff, 2001; Chace & Walsh, 2006; Sol *et al.*, 2014) and other organisms (McKinney, 2008; Luck & Smallbone, 2010; Knop, 2016). However, it contrasts with another previous global-scale study on avian assemblages which did not find support for this effect (Pautasso *et al.*, 2011). The reason for this difference might be our selection of papers presenting simultaneously urban and nonurban assemblages, while Pautasso *et al.* (2011) compared independent studies for each habitat. In general, our study presents another piece of evidence indicating that the number of bird species is reduced in urban habitats in comparison with nonurban habitats.

Our results on global evolutionary distinctiveness support those obtained by Morelli *et al.* (2016) for European bird communities, clearly showing that urbanization also affects other components of avian biodiversity (phylogenetic diversity) other than species richness. The reduced avian phylogenetic diversity associated

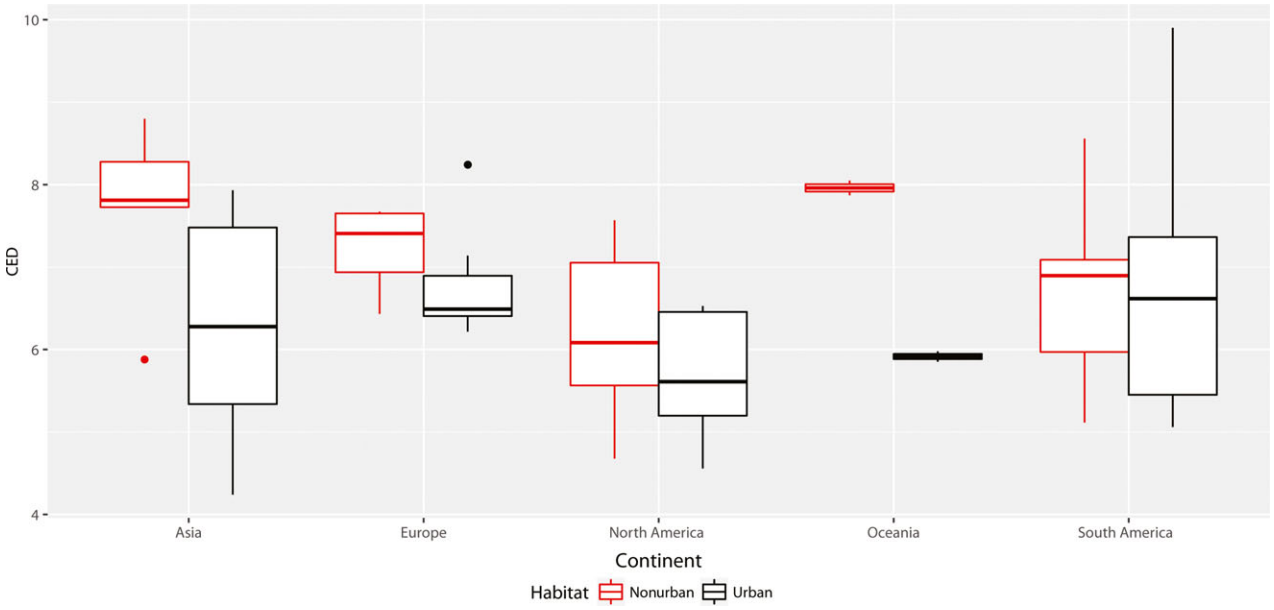

Fig. 4 Comparison of community evolutionary distinctiveness between habitats in each continent. The *y*-axis represents the estimated variable. The boxplots show the median (bar in the middle of rectangles), upper and lower quartiles, maximum and minimum values (vertical lines), and outliers. [Colour figure can be viewed at wileyonlinelibrary.com]

with urban landscapes could have important conservation implications, such as reorienting our conservation efforts to prevent the loss in evolutionary information (Mace *et al.*, 2003; Winter *et al.*, 2012). Phylogenetic diversity is a good surrogate for species rarity and can be used as complementary information for conservation plans by identifying and prioritizing those species in need of protection (Winter *et al.*, 2012) or the best targets to retain a major proportion of evolutionary history in urban bird communities. It will also be very interesting to test whether other organisms are impacted in a similar way. Birds are good predictors of abundance of other vertebrates (Rodrigues *et al.*, 2007), and even if invertebrates follow a similar pattern of reduction in species richness due to urbanization (McKinney, 2008; Knop, 2016), they might differ regarding other components of biodiversity. Plants are particularly interesting organisms in this respect because of the structural role that they play in cities (Groffman *et al.*, 2014) and the different patterns (in comparison with animals) that manifest due to urbanization (increase in overall species richness, but reduction in native vegetation), particularly because of the introduction and growth of non-native species in urban areas (Palomino & Carrascal, 2006; McKinney, 2008; Luck & Smallbone, 2010; Čeplová *et al.*, 2015). Furthermore, it has been shown that the high species richness of urban flora in Germany was not reflected in high phylogenetic distinctness suggesting that these two measures of biodiversity are not directly related (Knapp *et al.*, 2008). Interestingly, a recent study has shown that urbanization seems to reduce phylogenetic diversity of urban plant communities in Central Europe, suggesting that the pattern observed in our study might apply to plants too (Čeplová *et al.*, 2015). Worth to mention is that habitat type (urban vs. nonurban) and not geographical predictors (latitude or longitude) explained our CED results which suggests that this effect is global and independent of the location. This is also supported by the shared pattern found for this biodiversity proxy in all continents (Fig. 4). However, these results contrast with those found by Morelli *et al.* (2016) showing a negative significant correlation between CED and latitude for European birds. It is possible that this pattern is restricted to Europe or that it only arises when cities from very high latitudes are included in the analyses. Only 4% of our cities were located higher than 55°N, compared with 50% of the locations from Morelli's European study. In addition to this lack of high altitude studies on urbanization, we found other geographical areas in which we should investigate this issue further (Fig. 1). Probably the clearest example is Africa, which in addition is going to be a great center of urban development in the forthcoming years (Seto *et al.*, 2012; McPhearson *et al.*, 2016).

Despite the general effect found for biodiversity, the expansion of urban landscapes is not completely homogeneous in all continents (Figs 3 and 4). Bird communities in South America seem to be the most affected in terms of taxonomic diversity, probably because the

native habitats in this continent hold the largest avian species richness in the world (Newton, 2003). Nevertheless, South American CED is not reduced so strongly, which suggests that some species with high evolutionary uniqueness are being retained in urban areas in this continent. Oceania shows just the opposite pattern being highly affected in terms of CED, much more than any other region (Fig. 4). This might be due to the small sample size of urban studies for this particular region included in our database, but could also indicate that cities in Australia and New Zealand are selectively removing evolutionary unique species. The latter alternative is of special concern considering that Australia and New Zealand are among the most important hot spots in evolutionary diversity of birds (Jetz *et al*., 2014). These differences between regions provide valuable information in order to design more efficient conservation plans and point out that conservation strategies should be adapted to the region to minimize the impact of urban land-cover expansion.

Another clear conclusion that could be extracted from our results is about biotic homogenization. We found strong evidence supporting the global taxonomical and evolutionary homogenization of avian communities (Fig. 2). This is in line with previous findings showing that urban birds are taxonomical, functional, and phylogenetically homogenized (e.g., Devictor *et al*., 2008; Reif *et al*., 2013; Godet *et al*., 2015; Morelli *et al*., 2016). This evolutionary homogenization of bird assemblages could happen because of exclusion of unique species, which will not be suitable to inhabit in urban areas, or due to many recent speciation events in cities (Morelli *et al*., 2016). Nevertheless, the latter option seems unlikely given that urbanization is a relative recent process in Earth's history (5000–6000 years, Gaston, 2010) and the majority of birds have evolved before humans gathered in settlements (>2.5 MYr, Jetz *et al*., 2012). Our results could suggest an association between recently diversified lineages and some traits that favor urban life (i.e., generalism, Müller *et al*., 2013), although the link between phylogenetic and functional diversity is not completely clear yet (Winter *et al*., 2012). For instance, Sol *et al*. (2014) showed that sensitivity to urbanization is not randomly distributed across the avian phylogeny, suggesting that there are some lineages of birds more prone to survive in urban areas than others. Furthermore, not only cities contain species with lower average evolutionary distinctiveness, but they also seem to impose an upper limit on evolutionary diversity of urban bird assemblages similarly to what happen with the number of bird species. The max ED is significantly lower in urbanized landscapes than in close nonurbanized areas (Table 1, Fig. 2) which support the biotic homogenization hypothesis. However, this result is difficult to explain in ecological terms and will need further research. One potential explanation could be the extirpation of lineages with extremely high ED values, which would be associated at the same time to those species with very particular requirements/adaptations (i.e., particular food or inability to fly). Alternatively, these high ED birds could be representative of locally restricted species (Webb & Gaston, 2000) which are most likely to not become urbanized (Bonier *et al*., 2007; Møller, 2014). However, correlations between breeding range size and avian ED are not straightforward and seem to be complex and multifactorial (Jetz *et al*., 2014). Our study investigated patterns at the community level; however, these patterns should have arisen as a consequence of differences among individuals (i.e., those less afraid to humans (Møller, 2008; Díaz *et al*., 2013)) and subsequently among species (i.e., those presenting certain traits that facilitate living in urban areas (Luck & Smallbone, 2010; Møller, 2014; Sol *et al*., 2014). Future work should aim to integrate these three levels (individuals, species, and communities) in order to completely understand the effect of urbanization on biodiversity.

Recent studies have highlighted that cities can host an important level of biodiversity (Müller *et al*., 2013; Aronson *et al*., 2014) and can also act as key reservoirs for threatened species (Ives *et al*., 2016). However, our results raise important conservation concerns given the significant and worldwide reduction in avian biodiversity associated with urbanization. Furthermore, our findings suggest that urbanization, like agriculture, is another human landscape change responsible for the global loss of evolutionary information (Frishkoff *et al*., 2014) and a key player in the homogenization of biotas. Our conservation efforts should aim at retaining a major proportion of biodiversity in cities (McPhearson *et al*., 2016; United Nations, 2016), in the case of birds, for example by increasing the native vegetation in urban areas (Aronson *et al*., 2014; Threlfall *et al*., 2016) or with particular conservation plans to retain species with high ED values (Winter *et al*., 2012). The different trends found for some regions between species richness and ED also suggest that more studies using different and complementary biodiversity measures are needed to fully understand how urbanization impacts biodiversity. We hope that our findings can be valuable for conservationists and policymakers when establishing conservation priorities and regulating urban expansion.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. List of sites used and associated information.
Table S2. List of species used and associated information.
Table S3. List of GLMMs performed in the study.